SYSTEMATICS OF *LINDLEYA* (ROSACEAE: MALOIDEAE)

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ABSTRACT

The genus *Lindleya* consists of a single species *L. mespiloides* Kunth in H.B.K. It is endemic to three arid regions in México: from southeastern Chihuahua, south to central San Luis Potosí and southwestern Tamaulipas; in Hidalgo-Querétaro; and Puebla-Oaxaca with outlying collections from northwest Guerrero. The genus has a complex taxonomic history involving multiple uses of the generic name; the generic name *Lindleya* Kunth is conserved. Data on leaf, flower, and fruit structure are provided. The taxon is quite uniform in floral and fruit-seed characteristics throughout its range, though it shows differences in leaf shape, leaf and sepal size with leaf sizes reflecting habitat. The genus is distinguished by its large flowers with asymmetrical petals, ±20, large, often folded anthers, its superior, perigynous ovary with 5 connate carpels, and its globose, loculicidally dehiscent woody capsules containing narrowly winged seeds. Comparisons are made between *Lindleya* and its nearest relative *Vauquelinia*. Molecular data supporting its relationship at the base of the tribe Pyreae (ex subfamily Maloideae) is discussed along with a call for further modifications of the classification of the Rosaceae.

RESUMEN

El género *Lindleya* tiene una sola especie *L. mespiloides* Kunth in H.B.K. Es endémica de tres regiones áridas de México: del sureste de Chihuahua, hacia el sur hasta la parte central de San Luis Potosí y suroeste de Tamaulipas; en Hidalgo-Querétaro; y Puebla-Oaxaca con colecciones distantes en el noroeste de Guerrero. El género tiene una historia taxonómica compleja que implica múltiples usos del nombre genérico; El nombre genérico *Lindleya* Kunth está conservado. Se aportan datos de la estructura de la hoja, la flor y el fruto. El taxon es bastante uniforme en las características florales, de frutos y de semillas en todo su rango, aunque muestran diferencias en forma de la hoja, tamaño de hojas y sépalos con tamaños de hoja que reflejan el hábitat. El género se distingue por sus flores grandes con pétalos asimétricos, ±20 anteras grandes a menudo dobladas, su vario súpero perigino con cinco carpelos connados, y sus cápsulas globosas, leñosas, dehiscentes, loculicidas, que contienen semillas estrechamente aladas. Se hacen comparaciones entre *Lindleya* y pariente más próximo *Vauquelinia*. Se discuten los datos moleculares que soportan su relación en la base de la tribu Pyreae (ex subfamilia Maloideae) junto con una llamada a otras modificaciones de la clasificación de las Rosaceae.

INTRODUCTION

The monotypic genus *Lindleya* (Rosaceae) consists of sclerophyllous, evergreen shrubs with conspicuous white flowers and distinctive, woody, 5-carpelled capsular fruit. It is native to the arid and semi-arid chaparral or matorral of Mexico, with populations known from Puebla-Oaxaca, Hidalgo-Querétaro and the mountains of the Sierra Madre Oriental and the Chihuahuan Desert from San Luis Potosí, Tamaulipas, Nuevo León, Coahuila and eastern parts of Zacatecas, Durango and Chihuahua.

The genus has a complex but interesting taxonomic history that is reviewed below. Data on vegetative and reproductive features are presented and illustrated along with a formal taxonomic treatment and distribution maps. The most interesting aspect of *Lindleya* is its place in the phylogeny of the Rosaceae. With its five-carpeled capsular fruit, its placement within the family has been problematic.

MATERIALS AND METHODS

The study is based on empirical observations from field-collected and herbarium material as well as extensive field studies. Herbarium specimens were borrowed from A, GH, MO, MICH, NY, TEX-LL and US. Additional data was obtained from collections from ARIZ, ASU, CAS, DS, ENCB, MEXU, RSA, POM during visits to those herbaria. Anatomical studies incorporated standard paraffin techniques (Johansen 1940) for production of serial sections of leaves and flowers. All plant measurements were made from dried material unless otherwise noted.

Taxonomic History.—The genus *Lindleya* was named by Kunth (1824) in the sixth volume of Humboldt and Bonpland's *Nova Genera et Species Plantarum* [5 Jan 1824-pertinent dates from International Plant Name Index (www.ipni.org) and Taxonomic Literature II (Stafleu & Cowan 1976–1988)] with a complete description. An illustration of the sole species, *Lindleya mespiloides* Kunth, was published in Apr 1824 (fig. 562). The genus was named for the then young John Lindley (1799–1865), British botanist, student of the Rosaceae and Orchidaceae, who went on to be professor of botany at the University College London (1829–1860).

However, prior to this, the name *Lindleya* had been used as a generic name several times. The first use of *Lindleya* as a genus name was by Nees von Essenbeck (1821), in a paper (21 May 1821) determining specimens from the Brazilian collections of Spix and Martinus. His *Lindleya* was a genus in the Theaceae, which Index Kewensis states is based on a species *Lindleya fruticosa* Nees (=*Laplacea semiserrata* Cambess.). Nees' *Lindleya*, however, is a homotypic synonym of a slightly older *Wilkstroemia* Schrader (5 May 1821) and thus is a superfluous name. Kunth in Humboldt, Bonpland *loc. cit.* (25 Feb. 1822) recognized this genus as *Laplacea* Kunth.

Kunth himself had previously used the generic name *Lindleya* twice. His first use was on plates of two species that were published in volume five of *Nova Genera et Species Plantarum*. According to Taxonomic Literature II, the fascicle of plates bearing the name *Lindleya* (plates 479–480) were published on 25 Feb. 1822, while the text, (vol. 5: 361–367) was not published until 24 March 1823, however, in the text, the species were placed in the genus *Casearia* (Flacortiaceae). The use of generic name *Lindleya* on the plates has been considered as a *nomen nudum* by Index Kewensis and Index Nominum Genericorum database and I.P.N.I. But the International Code of Botanical Nomenclature (McNeil et al. 2006) Art. 42.3 considers an illustration with analysis (i.e., with separate figures showing details to aid with identification) as being acceptable in place of a written description or diagnosis for a species description. But Art. 42.1, 42.2 notes that this can apply only if the genus is monotypic. As there were two species illustrated, the use of *Lindleya* here can be considered as a *nomen inval.*

Kunth (1822) again used a *Lindleya* in his brief treatise on Malvaceae, Büttneriaceae and Tiliaceae (20 Apr, page 10) listing "Lindleya nob." ("nob." indicating nobilis, or himself; see ICBN recom. 46D) between *Theobroma* Linn. and *Guazuma* Plum., in Sectio [subfamily] II "Büttneriaceae verae" of Büttneriaceae (once Sterculiaceae, now Malvaceae s.l.). This is purely a listing of a known or proposed name and again is a *nomen inval.*, without description given, implied or cited.

Rydberg (1908a) in his Notes on Rosaceae preceding his North America Flora treatment (Rydberg 1908b) listed the previous use of *Lindleya* by Kunth and Nees (as noted in Index Kewensis) and offered a new generic name *Lindleyella* for the Rosaceaous genus, and described a second species *L. schiedeana* Rydb., characterized by more obovate leaf blades and longer, more obovate petals. In 1940 Fedde, for some reason, rejected the earlier *Lindleyella* of Rydberg (1908), in favor of a later described *Lindleyella* Schlechter (1914), a genus of Orchidaceae with five species that were named from 1914 to 1924, and substituted a new name, *Neolindleyella* Fedde for Rydberg's genus. As to why Fedde would choose a younger name (*Lindleyella* of Schlechter 1914) against an older name (*Lindleyella* of Rydberg 1908) is unknown as it goes against the rules of priority, which he so strongly espoused. Fedde's work on botanical nomenclature had become such a disruption on nomenclatural stability that the provision for conservation of generic names was enacted during the Vienna Congress in 1905 (Briquet 1906).

In 1930, at the fifth International Botanical Congress (Briquet 1935), the rule concerning homonyms was altered. Prior to that time, a later homonym could be accepted as a valid name if the earlier name had become a synonym and was not being used. The fifth congress maintained strict nomenclatural priority and rejected later homonyms with the understanding that all well known generic homonyms, as far as possible, should be conserved.

To this end, a systematic search was made to validate later homonyms via generic conservation (Rehder et al. 1935). The task was assigned to various botanists each responsible for genera based on alphabetical groupings. Genera beginning with the letters L through P were assigned to Dr. Rudolf Mansfield of the Botanical

Museum of Berlin. Through his work, *Lindleya* Nees was rejected in favor of *Laplacea* H.B.K. (nom. cons.). Kunth's use of *Lindleya* as a replacement name for *Casearia* was considered a *nomen nudum*, and *Lindleya* of Kunth in Humboldt and Bonpland (1824) was conserved against *Lindleyella* Rydb. (Green 1940). Thus the correct name for the genus, under the present rules, following that round of conservation, would be *Lindleya* H.B.K., or following those who object to the H.B.K. designation, *Lindleya* Kunth in Humboldt & Bonpland (*nom. cons.*) or just *Lindleya* Kunth following ICBN 2006, Art. 46, ex. 9, note 1 (McNeill et al. 2006).

Of interest, in 1858, J. Agardh, in his *Theoria Systematis Plantarum*, placed *Lindleya* in its own family Lindleyaceae J. Agardh. In the same paper, he also recognized Cercocarpaceae J. Agardh, Coleogynaceae J. Agardh, and many other new families of dicotyledoneae.

MORPHOLOGY AND ANATOMY

Growth habit.—The species is a multi- to few-stemmed shrub (Fig. 1A). In more mesic habitats, the main branches are ascending and the plant forms an obovoid-spreading shrub to 2–4(–5) m tall with the uppermost branches either ascending or arching outward. In dry habitats the plants form more rounded, densely and divaricately branched shrubs to 1.3 m tall and wide. These arid-land shrubs may be misshapen due to browsing by goats, or somewhat thorny due to the placement of dried lateral stems.

Stems.—Stems are heteroblastic. Young long-shoot stems are initially maroon, glabrous, with internodes 7–15 mm long. They develop a single band of vascular tissue and dense strands of primary phloem fibers. The cortex and pith cells both develop thickened walls. Secondary growth initiates soon after stem development. Short-shoots develop from the nodes. As they mature they may develop into variously branched short-shoot systems to 1–5(–7) cm long with internodes 0.4–1.5(–5) mm long. The epidermis of young stems is soon replaced by a light gray periderm. Older branches have a smooth gray periderm marked by distinctive horizontal lenticles (Fig. 1D).

Stipules.—Paired yellow-green stipules occur at each long- and short-shoot node at the margins of the canaliculate petioles. They are typically acicular, 0.4–0.9(–2.2) mm long and are bordered on two sides by well-spaced or crowded, distinct, reddish-maroon multicellular glands to 0.2–0.3 mm long (Fig. 3A). When shorter, the crowded glands, which decrease in size acropetally, make the stipules appear more deltate. When longer, the stipules are very slender, acicular with well spaced marginal glands. The stipules mark the separation of the broadened leaf base from the canaliculate petiole and occur just below the zone of leaf abscission. The petioles receive three traces from the stem.

Leaves.—Leaves range from leptophylls, 8 mm long 2.5 mm wide to mesophylls 55 mm long and 17 mm wide (Fig. 2B–Q). The lamina range from narrowly oblanceolate, narrowly obovate to obovate. The apices range from narrowly acute, obtuse, rounded, to retuse often with an acuminate to mucronate tip. Any one plant may have some leaves with acute tips, other leaves with rounded tips. They are cuneate at the base with the margins forming decurrent narrow wings along the short, canaliculate, yellowish petioles. The margins are crenate; the crenations are gland tipped, with rounded distal and proximal margins. The crenations are usually uniform in distribution, but are more widely separated along the lower blade margins. The leaf blades are glabrous throughout. The marginal dark red-maroon glands are compressed ovoid, sessile, the marginal ones ascending towards the tip, the distal ones erect, 210–290(–350) μm long, to 100–120(–160) μm wide at the broad base. The gland's marginal cells are anticlinally elongated. The glands fall from older leaves.

The dorsi-ventral leaf blades are generally ascending, with the adaxial surface slightly concave (Fig. 1B). The blades range from 220–360(–430) μm in trans-section thickness and are 350–400(–430) μm thick at the midvein. The midvein is raised on both the adaxial and abaxial surface proximally, but only on the abaxial surface in the mid section and distally, except in the thickest blades where the midvein is not raised (Fig. 2A). The adaxial epidermis usually consists of large polyhedral cells that undergo a periclinal division, producing a narrow external cell with rather dense cytoplasm and a much larger internal water-storage cell. The outermost wall of the upper epidermal cell is about 5.5–7 μm thick, with the cuticle 4–5.6 μm in thickness. The abaxial epidermis has similar structure under vascular bundles, but in the intervascular area they consist of a mix of

FIG. 1. Photographs of *Lindleya mespeloides*. **A.** Growth habit of shrub ca. 2.5 m tall (lower branches have been removed by goats). **B.** Young stem showing ascending orientation of leaves. **C.** Flowering branch, showing density of flowers. **D.** Trunk of stem about 11 cm in diameter showing smooth gray bark with conspicuous lenticels. **E.** Flower bud showing bract, pedicel, sepals with bordering glands. **F.** Mature flower, face view, showing oblique, white petals, 20 stamens and central ovary. **G.** Mature flower, lateral view, showing ascending disposition of stamens. A, B, D from near Iturbide, Nuevo León, México (*Henrickson 22112*, TEX), C, F, G from near 18 de Marzo, Nuevo León, México (*Henrickson 22118*, TEX). Scale in B = 5 cm, in C = 10 cm, in E = 5 mm, in F & G = 1 cm.

epidermal and guard cells and the structure is difficult to sort out. The epidermal cells are larger and have a smaller external cell, but the guard cells do not. The adaxial leaf mesophyll consists of 2(–3) layers of crowded palisade cells. A palisade-type cell orientation may or may not occur in the abaxial mesophyll, but cells are not as dense. The primary, secondary, and usually tertiary veins have vascular cambia. A mass of support cells develops adaxial to the phloem. In some leaves these consist entirely of collenchyma cells, in others collenchyma mixed with fibers, and in the primary and secondary veins consist of masses of lignified fibers. Usually a collenchymous bundle-sheath extension occurs both above and below the primary-secondary-tertiary veins and sometimes bundle sheath extensions continue to the fourth and fifth order veins (seen throughout the
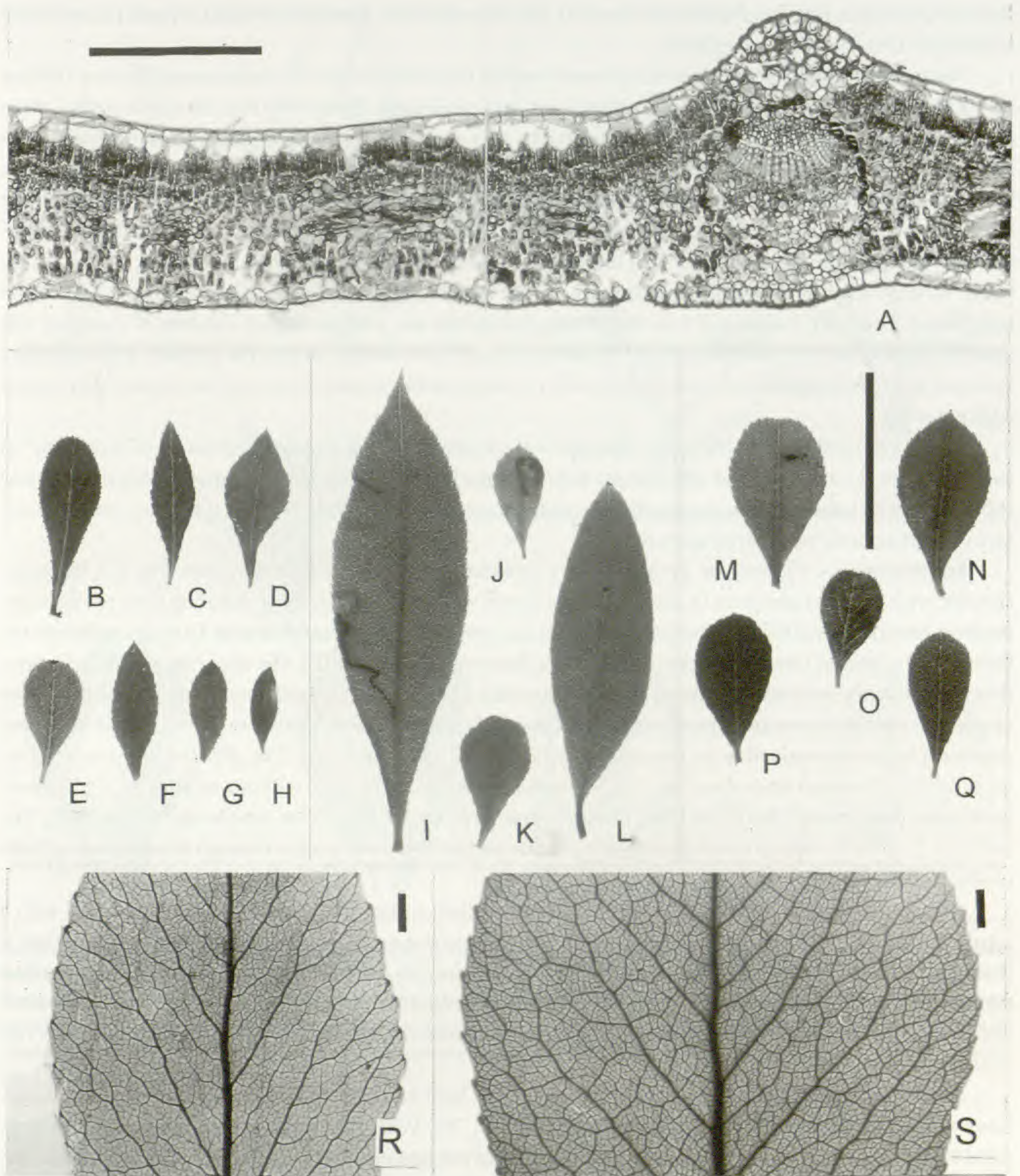
Fɪɢ. 2. Leaf structure of *Lindleya mespeloides*. **A.** Transverse section of leaf showing bi-layered upper epidermis, palisade and lower palisade-like spongy mesophyll. Note midvein is raised on adaxial (upper) leaf surface. **B–Q.** Photographs of wetted leaves showing variation of size and leaf shape from specimens from Coahuila-Nuevo Leon (B–H), Hidalgo (I–L), and Puebla-Oaxaca (M–Q). **B.** *Henrickson 22056* (TEX)-NL, **C.** *Henrickson 6225* (TEX)-Coah. **D.** *Johnston et al. 11465* (LL)-Dgo. **E.** *Steward 294* (GH)-Coah. **F.** *Steward 378* (GH)-Coah. **G.** *Henrickson 22062* (Tex)-LL. *Stanford et al. 626* (GH)-Tamp. **I.** *González 21443* (F)-Qto. **J.** *González 2401* (LL)-Hgo. **K.** *Gold 324* (TEX)-Hgo. **L.** *Moore 2481* (GH)-Hgo. **M.** *Salinas & Solis 3238* (TEX)-Oax. **N.** *Tenorio 6882* (TEX)-Pue. **O.** *Dorado & Salinas s.n.* (Tex.)-Pue. **P.** *Tenorio 18341* (TEX)-Oax. **Q.** *Tenorio González 18341* (TEX)-Oax. **R–S.** Leaf clearings. **R.** *McVaugh 10346* (US). **S.** *Gonzalez 1443.* (MEXU). Scale in A = 0.3 mm, in B–Q = 20 mm, in R–S = 1mm.

states of Querétaro, Hidalgo, Puebla, and Oaxaca). The mesophyll has scattered cuboidal crystals that are more common in bundle-sheath extensions.

Venation, as seen in cleared leaves is pinnate, weakly brochidodromous to semicraspedodromus (Ellis et al. 2009). The primary vein is straight, symmetrical, and moderately thickened (Fig. 2R–S). Secondary veins are irregularly alternate, extending from the primary vein at angles of 20–40 degrees. In narrow leaves they tend to arch slightly towards the tip but do not extend to the leaf tip. The secondary veins exhibit moderate branching towards the margins, often forming through connections with adjacent secondary veins one or more series of arches below the margins, with the crenations served by tertiary or smaller veinlets. Intersecondary veins are composite and muched branched, connecting to the lower portions of adjacent secondary veins. Tertiary veins form random reticulations, mostly at right angles to the secondaries; they are percurrent and forked. There are 5 orders of vein branching; the areoles are well developed, random, 4–5 angled, the smallest veinlets are 1–3 times branched. Venation of small leaves differs in that the primary and secondary veins are much thicker than the tertiary and smaller veinlets, and secondary veins may not connect with super-adjacent veins.

Stomata are restricted to the lower (abaxial) leaf surface and range in number from 96–175 per mm^2 in small leaves ca. 13 mm long, and 140–175 per mm^2 in larger leaves to 27 mm long. Stomata do not occur below the veinlets with bundle sheath extensions. The stomata are usually subtended by four subsidiary cells. Subsidiary cells are anomocytic in arrangement.

Inflorescences.—Flowers are usually solitary terminating new growth of the season (Fig. 1C), but occasionally, with vigorous new growth, more than one flower will develop, with the subtending flower(s) developing from lateral shoot(s) from a subterminal node in the new growth of the same season. In such conditions the flowers will appear to form simple corymbs or three-flowered cymes (Fig. 1E). The uppermost, reduced leaves, that form with the season's growth are typically crowded below the flower and extend onto the pedicel. The uppermost cauline leaves are typically only 8–18 mm long, petiolate with slender to deltate, gland-margined stipules. They have canaliculate petioles and gland-margined, glabrous blades (Fig. 3B). The uppermost leaves are reduced to linear to lanceolate bracts to 3–5 mm long, 0.5–1.2 mm wide, without stipules but with glands continuing from the petioles to the blade margins. True pedicels, when present, may be up to 2 mm long. The terminal flowers disrupt terminal growth of a shoot, continued growth occurs through development of subtending lateral shoots.

Flowers-Hypanthia.—Pedicels terminate in thick-walled, coriaceous, obconic, hypanthia topped with 5 sepals, 5 petals and about 20 stamens (Figs. 3C, 5A). The ovaries are not attached to the hypanthia except at their sessile bases. The free portion of the hypanthia is about 0.7–1 mm in thickness. The outer hypanthial surface is light green, glabrous and shiny. The inner surface is yellowish-green in color, nectariferous, sometimes vertically ribbed (the ribs reflecting the position of stamen traces), with a somewhat expanded inner rim subtending the filaments.

Sepals.—The hypanthia terminate in five coriaceous, light greenish, broad-based, ovate to oblong-ovate, lance-ovate, usually acuminate, imbricate sepals (Figs. 1E, 3B). Where the sepal margins overlap, underlying sepal margins are membranous to 0.5(–0.9) mm wide and are sometimes cordate at the broad sepal base. The external or overtopping sepal margins are usually not membranous but usually have distinctive reddish glands similar to those found on leaf margins. The sepal tips usually terminate with a reddish gland. The sepals may be glabrous throughout the abaxial surface or variously villous distally. The inner surfaces typically are glabrous in the lower half but distinctly villous distally and along the distal margins, with slender, crinkly, white hairs to 0.6(–0.9) mm long. There are some differences in sepal size throughout the range of the species; plants from Oaxaca-Puebla tend to have shorter sepals, but this is not consistent as similar short sepals occur in small flowers throughout its northern range. Sepal size usually reflects overall flower size, and flower size can vary with environmental conditions. The sepals usually persist on the rim of the hypanthium as ascending or reflexed structures (Fig. 3G).

Petals.—The five broadly obovate, broadly clawed petals are borne equally along the hypanthium rim alternate to the sepals. The petals are spirally arranged in bud and are oblique distally with the portion of the
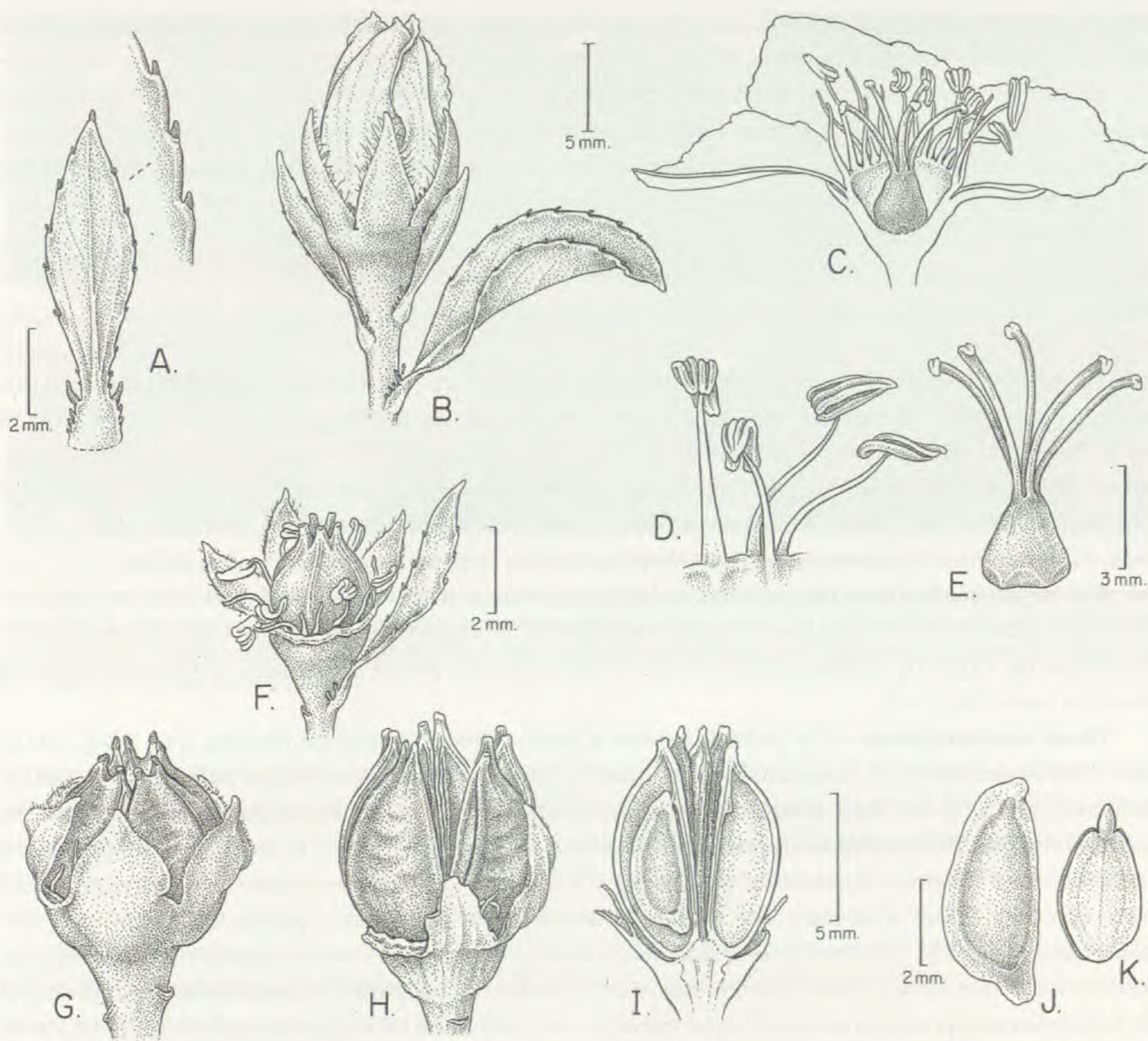
Fig. 3. Flower, fruit, and seed structure of *Lindleya mespeloides*. **A.** Floral bract showing marginal and basal glands and paired stipules. **B.** Preanthesis flower with subtending small leaf and bracts. **C.** Longitudinal flower section showing hypanthium and sessile ovary. **D.** Stamens at rim of hypanthium. **E.** Sessile ovary with styles and stigmas. **F.** Immature fruit, note subtending hypanthium, persistent bract, 5 style bases. **G.** Partially open fruit surrounded by dry hypanthium and sepals. Note the style bases have been split apart. **H.** Post-dehiscent fruit with some sepals removed showing dehisced carpels. **I.** Longitudinal view of mature fruit with carpel interior exposed showing seed. **J.** Seed. **K.** Embryo. Magnifications as indicated. A–E (*Henrickson 22112*, TEX); G–K (*Henrickson 22222*, TEX).

petal that develops under adjacent petals being much larger than the portion exposed in the bud (Figs. 1F, 5C). In most petals the right half of the petal is interior in bud and largest. But this will vary from flower to flower on one plant, with occasional flowers having the left half of the petal interior and larger than the right half. The petals are white, waxy appearing, well veined, thickened at the base, and thinning towards the sometimes crinkled margins. They spread outward at anthesis (Fig. 1F) and tardily abscise after anthesis. The mid vein often terminates in a single gland. When clearing the petals, the thick basal portion of petal often stains dark—it may be the source of the sweet floral aroma.

Androecia.—Flowers typically have 20 stamens borne at the inner rim of the hypanthia in one series or occasionally in two weak series with occasional smaller stamens born inside larger outer series of stamens (Fig. 3D). The inner and outer stamens usually develop opposite the petals with the interior stamen having a shorter incurved filament. The white filaments are acicular, very broad at the base, tapering distally. The filaments are attached to the mid-portion of the versatile anthers (Figs. 3D). Anthers are introrse in bud, 1.5–4 mm

long, oblong, apiculate at the tip, with two truncated basal lobes. Anthers are light yellow, longicidal, with 4 anther sacs, and the medial septa between the anther sacs appears to be secretory (glandular) as it is dull reddish in color (in dried anthers) and stains strongly in microscope slides. Within the buds, the outer, larger stamens are erect with straight anthers, while the inner stamens have inflexed filaments as their anthers develop further within the crowded hypanthial cup. These inner anthers are typically bent below the attachment to the filaments (Figs. 3D). They usually retain this shape at anthesis.

Gynoecia.—The compound ovary is 5 carpeled, ovoid, glabrous, slightly 5-angled in transverse section. The gynoecium is sessile at the receptacle apex (Figs. 3C, 5A) and the carpels are united ventrally up to the level of ovule insertion forming a thick-walled compound ovary with axile placentation (Fig. 6D). The carpels are laterally united from the dorsal edge to near the ventral margin. The carpels, however, are not connate centrally where a five-lobed opening extends to the base of the ovary (Fig. 4A). Sterling (1966) noted that this is a carpel fusion pattern similar to that found in the Maloideae. He also noted that occasionally the carpels will not be fused ventrally. Each carpel contains two apical, pendent, collateral ovules, about 0.7–1 mm long attached at the inner tip of the locule and receiving a downward-oriented vein from the adjacent ventral trace (Fig. 5A). The short, thick funiculus appears to function as an obtruator. The ovules have a broad outer integument, a thinner inner integument, and the embryo sac is quite large with a crassinucleate nucellus.

The carpels are free from the inner hypanthium walls except at the very base. The five styles are separate, terminal, slender, cylindrical and are obliquely expanded at the stigmatic tip (Fig. 3E). A split develops across the oblique tip, exposing papillate interior tissue. Dried styles may persist on the fruit, or they may break off above the bases (Fig. 3F–I).

Floral vascularization.—The pedicel contains a single cylinder of vascular bundles (Fig. 5E–1). At the base of the hypanthium, 10 (occasionally more) traces separate from the central traces and extend up the hypanthium (Fig. 5E-3–4). These produce an irregular series of lateral traces that extend horizontally into the hypanthial tissue. The hypanthial traces branch in the mid to upper hypanthium to produce additional stamen traces (Fig. 5D). The traces opposite the sepals typically divide to form 2 stamen traces that then pass parallel to the eventual medial sepal trace. The traces alternate with the sepals (i.e., opposite the petals) may also branch near the mid-hypanthium to form additional stamen traces, or one or more stamen trace may separate from the trace near the top of the hypanthium. In addition the trace opposite the petal divides near the top of the hypanthium to produce two lateral sepal traces, one to each of the two adjacent sepals (Fig. 5B, D). At the rim of the hypanthium, the 5 sepals then each receive one medial trace and two lateral traces derived from adjacent petal traces. The lateral traces each divide into two or three separate traces at the base of the sepal, which then has five or more parallel traces that extend up through the sepal base and branch above (Fig. 5B). The petals each receive a single basal trace that quickly divides into five to seven traces. These continue to branch and anastomose further up the petal in a pattern as shown in Fig. 5C. The 20 stamens each receive single traces that, as noted above, separate from the original 10 hypanthial traces at some point in the mid to upper hypanthium.

The central traces remaining after the initial hypanthial traces diverge, form into five central packets (Fig. 5E-5–6). From this mass, five dorsal traces diverge opposite the sepal traces receiving tissue from two adjacent masses of vascular tissue (Fig. 5E–6). These leave behind five dense masses of vascular tissue that becomes the 10 inner ventral carpel traces (Fig. 5E–6). The dorsal traces continue upward along the ovary periphery. They give off series of branch traces to the ovary wall, but disposition of these lateral traces is obscured by the densely staining, tannin-containing cells of the developing ovary wall. The ventral vascular tissue forms ten ventral traces that continue up the inner portion of the ovary to a point where they approach the dorsal traces at the style base. The traces to the ovules extend downward from this point to the funiculi and ovules (Fig. 5A). As noted by Sterling (1966), no wing traces diverge from the ventral traces at this time.

Fruit.—Fruits are globose, five-ribbed, 5-carpelled, woody, loculicidal capsules, subtended in the lower one third or one fourth by a separate leathery hypanthium ringed with persistent ascending or deflexed sepals and filament bases (Figs. 3-F–I, 6A–D). The style bases remain at the fruit tip forming a series of apiculate tips.
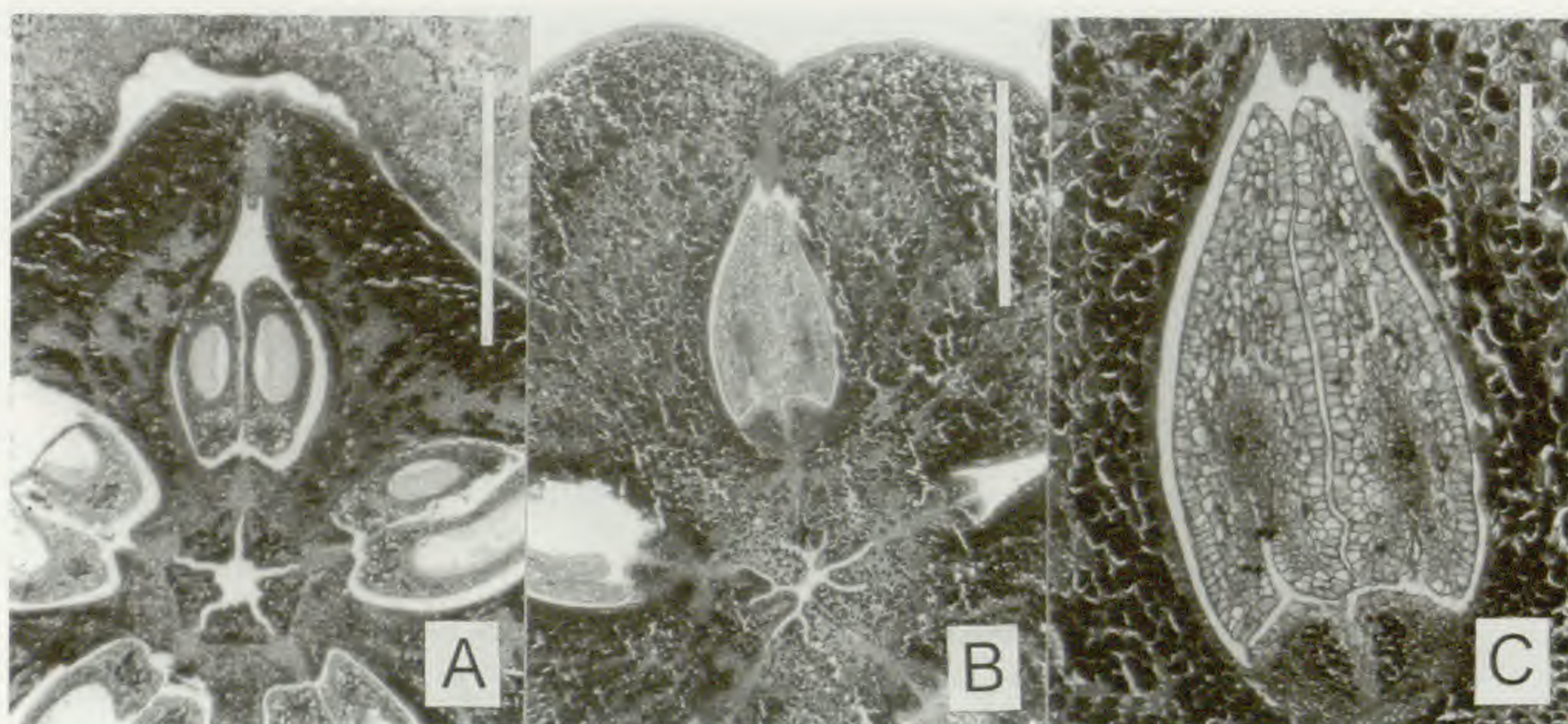
Fig. 4. Flower structures of *Lindleya mespeloides*. **A.** Transverse section of mid-compound ovary showing the paired ovules. Note the carpels are completely fused. **B.** Transverse section of upper compound ovary showing uppermost portion of ovary. The developing fruit wall in this area has many tannin-filled cells. **C.** Transverse section of upper portion of two ovules from B. All from *Henrickson 22118*, TEX (Galeana area, Nuevo León, México). Bar in A = 1mm, in B = 0.5 mm, in C = 0.1 mm.

At maturity, the carpels dehisce loculicidally directly through the ventral traces, splitting the ventral traces and the base of the style through a suture that is visible even in the developing ovary wall (Fig. 6A). The dehiscence splits the style bases in half, and continues onto the distal portion of the abaxial fruit surface (Fig. 3G–H). The inner lateral walls of the carpels are smooth and cartilaginous (as in an apple), lined with a single layer of macrosclereids 100–120 μm thick and subtended by a thick layer of brachysclereids each 35–65 μm in diameter with lignified walls 11–22 μm thick (Fig. 6E). The highly lignified tissue extends 1.5 mm in radial thickness in the triangular segments between the locules. Only the outermost 0.5 mm of the abaxial-most portion of the triangular carpel segments is not lignified.

Seeds.—Two compressed, half-ovoid, dull-brown seeds are produced in each locule. The seed shape conforms to the locule space, being straight along the ventral edge and rounded on the dorsal edge, with one flattened surface (where contacting the adjacent seed) with the outer surface convex (Fig. 3J, 6G). The seed coat is dull, light brown, and thin; the innermost cells attached to the embryo have many irregularly rectangular crystals (Fig. 6F). The embryo is oriented with the hypocotyl superior to (i.e., above) the cotyledons. The embryo, occupies about 70 percent of the total seed length, leaving a thin wing, 0.2–0.5 mm wide, at the dorsal margins. The embryo consists of two compressed, oblong cotyledons and a smaller, obovoid hypocotyl (Fig. 3K). Endosperm is absent at maturity. The seeds are wind dispersed. Upon germination the cotyledons form the first seed leaves of the seedling.

TAXONOMIC TREATMENT

LINDLEYA Kunth Nov. Gen. Sp. [H.B.K.] 6:240 (ed. qto.); 188 (ed. fol.). 1824 (nom. cons.), non *Lindleya* Kunth Nov. Gen. Sp. [H.B.K.] 5, t. 480. 1821, (nom. rejic.) = *Casearia* Jacq. (Flacourtiaceae); non *Lindleya* Nees, Flora 4:299. 1821, (nom. rejic.) = *Laplacea* (Theaceae); *Lindleyella* Rydb., N. Amer. Fl. 22(3):259. 1908; *Neolindleyella* Fedde in Repert. Spec. Nov. Regni Veg. 48:11. 1940. Type species: *Lindleya mespiloides* Kunth.

Evergreen, multistemmed shrubs; periderm gray, smooth. Stems heteroblastic, tending to form shortened axillary spurs in arid conditions. Leaves simple, alternate; leaf bases short, the stipules acicular to deltate, maroon, sometimes with marginal glands; leaf blades narrow to broadly oblanceolate to obovate, ovate, acute to rounded, sometimes retuse at tip, cuneate with the margins decurrent on short petiole, the margins closely crenate, the marginal teeth terminating in distinct glands, the blade coriaceous, shiny green, glabrous on both surfaces,
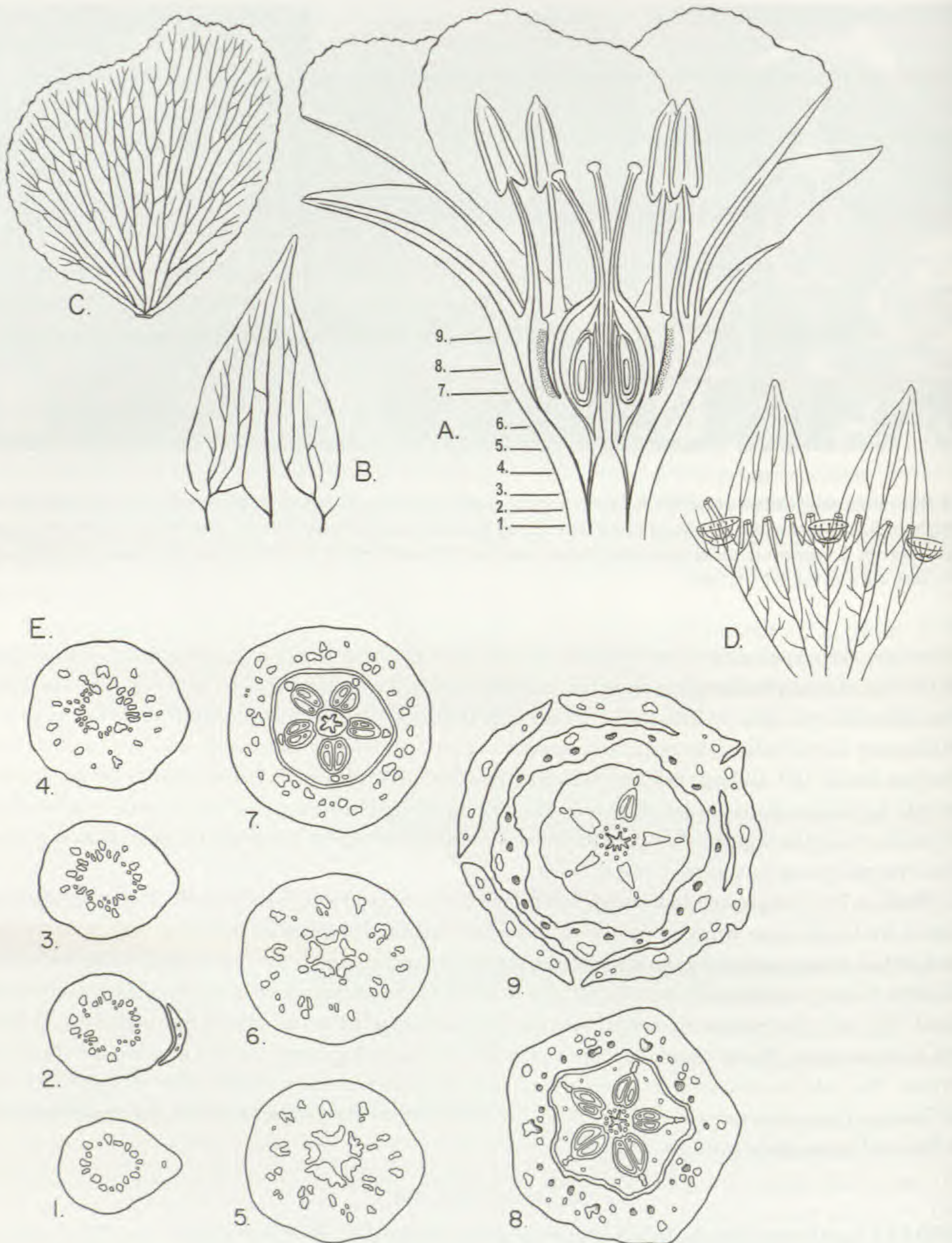
Lindleya mespelioides

Fig. 5. Flower vascularization of *Lindleya mespeloides*. **A.** Longitudinal section of flower indicating vascularization in hypanthium, ovary and relative position of ovary to hypanthium (number of stamens reduced for clarity). **B.** Vascularization of sepal. **C.** Vascularization of petal (traced from photograph). **D.** Characteristic pattern of vascular branching in hypanthium showing vascular traces to stamens, petal bases and sepals. **E.** Vascularization pattern of flower as obtained from serial transverse sections at progressively higher portion of flower from pedicel (1), to ovary base (7), into upper ovary where sepals are separating from hypanthium (9). All from *Henrickson 22118*.
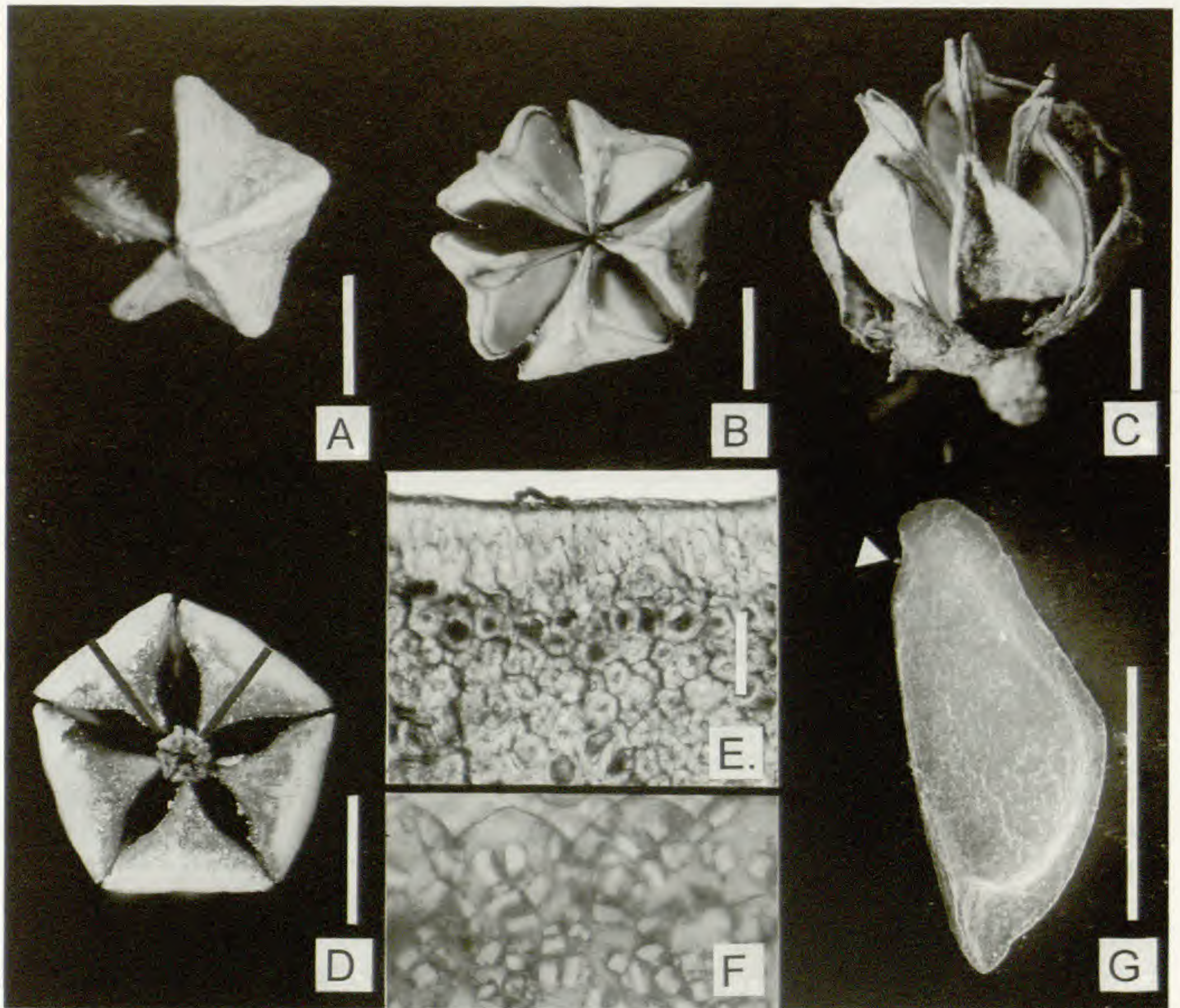
Fɪɢ. 6. Fruit and seed structure of *Lindleya mespeloides*. **A.** Top view of immature dried fruit showing five ridges that contain the dorsal traces. **B.** Top view of open loculicidial dehiscent fruit (without seeds). **C.** Lateral view of open fruit showing lower sepals and opened carpels. **D.** Transverse section of mature fruit showing five locules. The two black lines indicate limit of a single carpel. Adjacent carpels are completely connate. **E.** Structure of inner carpel wall consists of one row of macrosclereids 100–120 µm thick, subtended by thick layer of brachysclereids (from free-hand section). **F.** Surface view of epidermal cells of seed coat showing dense crystals. **G.** SEM micrograph of seed with characteristic narrow wing. Point of attachment to funiculus is indicated by arrow. (All *Henrickson 22056*, TEX). Bars in A–D, E = 3 mm, E–F = 100 µm.

major veins with bundle sheath extensions, venation brochidodromous to semicrospedodromus. Flowers complete, perigynous, usually solitary and terminal on long and short shoots, these sometimes forming terminal corymbs when the shoots aggregated or on long-shoot stems; bracts reduced, linear, gland-margined, borne on upper pedicel; hypanthia obconic, hemispherical in fruit, green, glabrous outside, nectariferous and yellow-green inside, coriaceous; sepals 5, imbricate, deltate to ovate, acute to acuminate, glabrous outside, villous near tip inside, somewhat coriaceous except along overtopped margins, spreading, persisting on fruit; petals 5, borne at the rim of the hypanthium, obliquely obovate, asymmetrical, white, spreading at anthesis, tardily deciduous, aromatic; stamens usually 20; filaments subulate, broadened at the base, borne at the inner rim of the hypanthium in a single (rarely two) series; anthers lanceolate, large, versatile, longicidal, yellowish; ovary superior (perigynous); carpels 5, in one series, antesepalous, completely connate laterally into an ovoid ovary; styles terminal, distinct, the stigmas terminal, oblique; ovules 2 per carpel, collateral, apically attached, pendent, the micropyles superior, the funiculi thickened, the tissue serving as an obtruator. Fruits spheroidal,

woody, loculicidally dehiscent capsules, the lower third surrounded by the coriaceous, persisting hypanthium, the carpels dehiscent distally along ventral and dorsal sutures, with thick, inwardly cartilaginous valves; seeds 2 per locule, compressed, narrowly winged abaxially, brown, the seed coat thin, the embryo with oblong-ovate, flattened cotyledons, the hypocotyl small, superior; endosperm absent. With one species.

Lindleya mespiloides Kunth, Nov. Gen. Sp. [H.B.K.] 6:240. 1823. *Lindleyella mespiloides* (Kunth) Rydb. N. Amer. Fl. 22(3):259. 1908. TYPE: MEXICO. HIDALGO: Inter La Puente de la Madre de Dios et vicum Magdalenae, (near Magdalena, ± 10.6 km ENE of Actopan, Hgo.), May (HOLOTYPE: P, fragment F!).

Lindleyella schiedeana Rydb. N. Amer. Fl. 22(3): 259. 1908. TYPE: MEXICO. HIDALGO: Inter Zimapan et San José del Oro; *Schiede s.n.* (HOLOTYPE: NY!). Distinguished by Rydberg as having more obovate (not oblong-lanceolate or oblanceolate) leaf blades 21–45 mm long, 11–21 mm wide, with acute, rounded to emarginate tips, and obovate (not rounded-obovate) petals about 15 (not 8–10) mm long. While the leaves of this collection are the widest observed among specimens examined, the type collection appears to represent a specimen of *L. mespiloides* with very large features. Other specimens from this region have much smaller or equally-large petals but smaller leaves. As noted above, leaf and flower size can be affected by environmental conditions. The type locality is about 80 km NW of that of *L. mespiloides*. As it is distinguished only by quantitative characters, its recognition is considered to be without merit.

Erect, much-branched, evergreen shrubs to small trees 1–3(–5) m tall, in dry habitats forming small, tightly, divaricately branched shrubs with many short shoots, in mesic habitats forming erect-ascending, moderately branched, tall shrubs; stems heteroblastic; long-shoot branches with internodes 7–15 mm long, glabrous, initially maroon, developing a close smooth, gray periderm; short-shoot branches 1–5(–7) cm long, variously branched, with internodes 0.4–1.5(–5) mm long. Leaves with petioles 1–2(–4) mm long; stipules 0.4–2.2 mm long, acicular to deltate, maroon, when longer more attenuate and bearing marginal glands; leaf blades narrowly oblanceolate, oblanceolate, spatulate, obovate, sometimes elliptical-oblanceolate, rarely somewhat ovate, (3.5–)11–32(–55) mm long, (1.6–)4–13(–21) mm wide, acute, acute-acuminate, rounded to emarginate at the tip, narrowly cuneate with the margins forming wings above the short petiole at base, the margins closely crenate to crenulate with 5–10(–15) teeth per cm of margin, the teeth each terminating in a maroon, conical gland 0.1–0.3 mm long, the blades coriaceous, glabrous throughout, shiny, dark green, slightly concave above, more yellow-green beneath, the midvein yellowish and raised on both surfaces. Flowers terminal, solitary on short, leafy shoots, rarely in terminal 3-flowered racemes, the subtending leaves reduced, the uppermost leaf(s) often reduced to linear, gland-margined bract(s) to 5 mm long; pedicels 1–2 mm long, glabrous, thick; hypanthia obconic, 4–5 mm wide (to 7 mm wide pressed), green, glabrous outside, yellowish-green, nectariferous inside above the ovary, the distal rim slightly expanded; sepals 5, ± imbricate, deltate to ovate, (3.3–)5–7(–9) mm long, (2.3–)3–4.5(–5.5) mm wide, acute to acuminate at the tip, coriaceous and green medially, with membranous whitish to pinkish margins 0.5–0.7 mm wide where overtopped, glabrous outside, glabrous at the base but densely villous near the tip inside and often villous-ciliate throughout the margins, the outer sepals sometimes with conical glands along the margins, the thin inner margins somewhat cordate at the base, the sepals spreading in flower and persisting around the fruit at maturity; petals broadly obovate to obovate-orbicular, obliquely asymmetrical distally, contorted in bud with the left (or right) margin of the petals overlapping the adjacent petals, the petals (7–)11–16(–19) mm long, (5.5–)11–14(–19) mm wide, spreading [the flowers (17–)22–40 mm in total diameter], obliquely rounded to emarginate at the tip, broadly cuneate above a very short and broad claw at the base, firm, thickish, waxy, white, spreading, emitting a sweet aroma, remaining on the flower well after anthesis, eventually deciduous, stamens usually 20; filaments linear-subulate, distinct, (2–)3.5–7(–8) mm long, to 0.5–0.8 mm broad at the expanded bases, borne in the inner rim of the hypanthium, of variable length and size with the shortest filaments occurring inside a larger filament opposite the sepals; whitish, glabrous throughout; anthers lanceolate (1.5–)2.5–3.5(–4) mm long, apiculate at the tip, cordate, the basal lobes often spreading or folded, ± versatile, reddish to usually dark yellow; ovary two-thirds + superior; carpels 5, completely connate, 2.5–4 mm high in the flower; styles 5, free to the base, 3.2–6.5 mm long, erect, stigmatic at the expanded tips. Fruits of woody, ovoid-spheroidal, long-persistent capsules, 7–10 mm long and wide, with the lower third surrounded by the persisting hypanthium, the carpels each loculicidly dehiscent in the distal two thirds, the locules radial, with cartilaginous interior lateral surfaces, the valves thick, woody, green, turning dark red to maroon, drying dark brown, glabrous; ovules 2 per locule, pendent;

seeds two per locule, oblong-ovate in outline, flattened, 4.3–6 mm long, 1.8–2.6 mm wide, narrowly winged on the curved abaxial margin, the adaxial margin straight; cotyledons ovate, endosperm absent, radical superior.

The species is characterized by its shrub to small tree growth habit with smaller plants of more xeric habitats often developing short-shoot branches and a somewhat thorny aspect, by its smooth gray bark, by its small to moderately large shiny green, mostly oblanceolate, acute to round-tipped leaves with gland-tipped finely crenulate margins, by its large terminal, sweetly aromatic flowers with a thickened obconic hypanthium that bears 5 glabrous sepals with thin villous-ciliate margins, 5 large, white, obliquely obovate to somewhat orbicular petals, and ± 20 stamens with subulate filaments and large versatile anthers, and by its superior, 5-carpelled ovary with 2 suspended ovules per locule, and 5 separate styles. The fruit are globose, woody, loculicidally dehiscent capsules with each locule producing two flattened seeds, each with a short wing along its outer margin. The flowers are conspicuous and remain on the plant after the anthers have shed their pollen creating a conspicuous floral display. The fruits are often long persistent, allowing recognition of the species in the field.

The species has three regions of distribution (Fig. 7): northern Oaxaca and adjacent Puebla, where it occurs oak-pine woodlands, chaparral and thorn scrub in association with species of *Malacomeles, Vauquelinia, Comarostaphylos, Rhus, Quercus, Juniperus, Pinus, Acacia, Leucanea, Beaucarnea,* and *Yucca* etc., from 1900–2400 meters elevation; in Hidalgo and adjacent northern Querétaro, where it again occurs from pinyon-oak-juniper woodland, chaparral association with many of the same genera. Its largest distribution is in the Sierra Madre Oriental and Chihuahuan Desert region from southwestern Tamaulipas, southern Nuevo León, northern San Luis Potosí, northern Zacatecas, northeastern Durango, the southern half of Coahuila and adjacent southeastern Chihuahua where it occurs in pinyon-juniper woodland, chaparral and canyons in desert scrub often in limestone, rarely gypseous or sandstone substrates in association with species of *Rhus, Garrya, Ceanothus, Fraxinus, Cercocarpus, Gochnatia, Vauquelinia, Berberis, Arctostaphylos, Quercus, Arbutus, Juniperus, Agave, Yucca, Dasylirion, Ungnadia, Leucophyllum, Condalia, Mimosa, Mortonia, Foresteria, Acacia,* and *Pinus* from 1100–2700 m elevation. Flowering typically occurs in May but may occur from March to September usually following rains, with occasional flowering occurring throughout the year.

Throughout the wide range of the species some notable variation occurs. Most apparent is the variation in leaf size. Most specimens from Hidalgo and Oaxaca have moderate large leaves 18–55 mm long, 8–18 mm wide. In contrast, most specimens from Coahuila and Nuevo León have smaller leaves, 10–26 mm long, 3.5–8 mm wide. The separation is by no means complete, as some specimens from both Hidalgo and Oaxaca also have small leaves. Leaf size corresponds to habitat, as plants in dry exposed areas have very small leaves that contrast with larger leaves of plants of nearby less-arid, shaded sites. As noted above, plants from Hidalgo, Querétaro, Puebla and Oaxaca have bundle-sheath extensions extending to the 4th and 5th order of vein branching in contrast to only the 1st, 2nd, and in part to the 3rd order of branching in more northern range. Specimens observed from Puebla and Oaxaca also tend to have shorter sepals measuring 3.0–5.2 mm long. In contrast, sepals from Hidalgo and northward specimens tend to be larger, (3.0–)4.5–7(–9) mm long, but there is considerable overlap, with sepal length corresponding to flower size and being variable even on a single specimen. Flowers range in total diameter (petal tip to petal tip) from 17 to 40 mm. Fruits also vary in size, with occasional specimens having fruits much smaller or larger than average.

PHYLOGENETIC RELATIONSHIPS

The placement of *Lindleya* within the Rosaceae has been problematic. Numerous subfamilial and tribal classifications of the Rosaceae have been proposed (Focke 1888; Hutchinson 1964; Schulze-Menz 1964; Cronquist 1981; Takhtajan 1987 1997, 2009; Kalkman 1988, 2004; Thorne 1983, 1992) etc. and most all retain four subfamilies, (some older treatments have five subfamilies with the inclusion of the Chrysobalanoideae, or six with the Neuradoideae) that corresponded well to fruit types: the Spiraeoideae, with follicles, (rarely achenes—*Holodiscus,* or capsules—*Vauquelinia, Lindleya*); Rosoideae with achenes (rarely druplets—*Rubus*); the Amygdaloideae with drupes (*Prunus* etc.), and the Maloideae (Pomoideae) with pomes (*Malus* etc.). Within these subfamilies, the treatments differed in the placement of genera within tribes. See summary in Potter et al. (2007).

Fig. 7. Distribution of *Lindleya mespeloides* in Mexico.

There has always existed a problem group of six genera with woody fruit and winged seeds some with follicles, others with capsules, consisting of: *Quillaja*, (plant polygamo-dioecious, fruit of five radiating woody follicles each with many (10–16) seeds in two series per carpel—northern South America); *Kageneckia* (dioecious, fruit with five separate follicles with many seeds in two series per carpel—western South America); *Vauquelinia* and *Lindleya*, (dry capsules with two-winged seeds per carpel—Mexico); *Exochorda* (plant polygamo-dioecious; fruit with five, rather compressed woody follicles—Eurasian) and *Lyonothamnus* (two follicles

with 1–4 non-winged seeds—California). Most classifications placed these within various tribes (Quillajeae, Exochordeae) within the Spiraeoideae.

Cytological Data.—As cytological data became available, it was found that the subfamlies had one or more base chromosome numbers with the Spiraeoideae having $x=9$, the Amygdaloideae $x=8$, the Rosoideae $x=7, 9$ (rarely 8) and the Maloideae $x=17$. The high chromosome number in Maloideae caused Sax (1931, 1932, 1933) and later Stebbins (1950, 1958) and many others (see Phipps et al. 1991; Rohrer et al. 1991, Cronquist 1981) to promote the view that the Maloids arose via paleo-allopolyploidy from $x=9$ Spiraeoideae and $x=8$ Amygdaloideae ancestors or from within the Spiraeoideae (Gladkova 1972).

In 1976 Goldblatt contributed chromosome numbers of several of the problem genera noted above. Of these *Exochorda* was found to be $x=8$, *Kageneckia* and *Lindleya* $x=17$; *Vauquelinia* $x=15$; and *Lyonothamnus* $x=27$ and *Quillaja* $x=14$. The high numbers in these taxa again gave clues that their relationship may lie with the Maloideae, and *Lindleya* and *Vauquelinia* were subsequently transferred to the Maloideae (Pyroideae) by Thorne (1983) and Takhtajan (1987). The 5-carpelled, dry-fruited *Exochorda* ($x=8$) was considered by Goldblatt (1976) to belonging to the $x=8$ Prunoideae, which has been supported by molecular data (Morgan et al. 1994). *Kageneckia* and *Quillaja*, which have similar appearing fruits, remained in subfamily Quillajeoideae (Thorne 1983; Takhtajan 1987).

Floral morphology Data.—Sterling (1966), on the basis of ovary morphology, considered the Quillajeae (containing *Exochorda*, *Kageneckia*, *Lindleya*, *Quillaja*, and *Vauquelinia*) to have sharp differences in the gynoecium structure and number and orientation of ovules. He noted that *Lindleya* had ovaries with complete lateral intercarpellary fusion of a type characteristic of the Maloideae, but with minimal hypanthium fusion. He also noted that the carpels of *Vauquelinia* were also maloid in nature though fused only basally and ventrally while being separate laterally.

Data from Rusts.—Savile (1979) summarized the use of fungus-host relationships in plant phylogeny. He notes that cedar-apple rusts *Gymnosporangium* occur throughout Pomoideae (Maloideae) with species also known from Myricaceae, Hydrangeaceae and from two genera of Spiraeoideae (*Vauquelinia* and *Porteranthus*— now *Gillenia*). He cites *Gymnosporangium vauqueliniae* Long and Goodding (1939) on *Vauquelinia californica* from Arizona and interestingly, *Gymnosporangium externum* Arth. & F. Kern in Arth., on *Gillenia* in eastern United States, which had been known since 1903. The on-line "Fungal Database" also gives references of *Gymnosporangium vauqueliniae* also on *Vauquelinia corymbosa subsp. karwinskii* from Nuevo León, Mexico and additional collections of *G. externum* on both species of *Gillenia* in the eastern United States (http://nt.ars.grin. gov/fungaldatabases). *Gymnosporangium* has not been reported on *Lindleya*.

Summary of non-molecular Data.—If we stop here and look at the data accumulated by the 1980s, we know that *Lindleya* has the same chromosome number as members of the then recognized Maloideae, and has some floral features in common with the Maloideae. We also have data from Cedar-apple rusts linking the related *Vauquelinia* with the Maloids. But confusingly, the rusts also occurred in another Spiraeoid, namely *Gillenia*. But as there was evidence that indicated that *Vauquelinia* and *Lindleya* were related to Maloids, there was no data indicating whether they were derived *from* the fleshy-fruited Maloids, or if they were basal to the fleshy-fruited Maloids. When we monographed *Vauquelinia* (Hess & Henrickson 1978), we had no evidence pertaining to the relative placement of *Vauquelinia* to the fleshy-fruited Maloids, so in that paper we concentrated just on species relationships. In the 1991 symposium on the Evolution in the Maloideae (Rosaceae) published in Systematic Botany, *Vauquelina* and *Lindleya* was not mentioned nor included in data sets (Phipps et al. 1991; Robertson et al. 1991). But by the mid 1990s, molecular data began to provide answers and laid the groundwork for a new phylogeny of the Rosaceae.

Molecular Data.—Molecular data presented by Morgan et al. (1994) from chloroplast rbcL sequences provided the first independent evidence for a needed subfamilial rearrangement of the Rosaceae. Their paper divided the family along the same lines as cytological data. Their data, however, showed that the old Rosoideae was polyphyletic, that the $x=7$ genera (*Filipendula*, *Fallugia*, *Geum*, *Waldsteinia*, *Potentilla*, *Fragaria*, *Agrimonia*, *Rosa*, *Rubus* and the $x=8$ *Alchemilla*) formed the core of the Rosoideae and the $x=9$ genera formed four distinct

groups: the Neviusia, Rhodotypos group; the Cercocarpus, Purshia, Lyonothamnus group; and the core Spiraeoideae with basal Spiraea-Aruncus-Holodiscus group, separate from a derived Physocarpus-Neillia group, and another Sorbaria group associated with Chamaebatiaria including the achene-bearing Adenostoma. Exochorda fell into the x=8 Amygdaloideae. Their data excluded the South American Quillaja from the Rosaceae.

Of significance to this paper, their data showed Kageneckia, Lindleya and Vauquelinia were basal to the remainder of the x=17 Maloideae, i.e., their data showed Vauquelinia and Lindleya, with capsular fruits, and Kageneckia with follicle-like fruits, as remnants of a clade that have given rise to the core Maloideae. That is, they were basal to the Maloids, not dry-fruited derivatives of fleshy-fruited Maloids.

Campbell et al. (1995), using the internal transcribed spacers (ITS) of the nuclear ribosomal DNA region, studied phylogenetic relationships within the Maloideae. Their study, however, concluded that the Maloideae was not monophyletic. They also noted that Vauquelinia forms a well supported clade with fleshy-fruited Eriobotrya and Raphiolepis that is the sister group to the remainder of the Maloideae. These data, however, were badly skewed, as their "Vauquelinia" sample was actually Raphiolepis collected at the University of Arizona campus by a graduate student, vouchered by a specimen collected twenty years earlier in 1975. Their data set did not include material of Lindleya, Kageneckia, and as it turned out, also did not contain Vauquelinia.

Data presented by Evans et al. (2000) on the "Granule-Bound Starch Synthase I" gene (GBSSI) provided further insights into the phylogeny of Rosaceae. The portion of this nuclear gene used (near the 5' end) consists of seven complete, short exons, and parts of two other exons alternating with non-coding introns. While all other diploid families in which this gene has been used, have only one GBSSI sequence, all diploid Rosaceae have two distinct sequences (designated as GBSSI-1 and GBSSI-2) that differ in the length of, or presence or absence of, the introns between particular exons providing evidence of Rosaceae monophyly. Species of Maloideae, with their higher chromosome number, have two copies or loci of each sequence, each of which have differences in their base-pair sequences that are designated GBSSI-1A and 1B, and GBSSI-2A and 2B. So there are six different sequences or loci, the GBSSI-1 and -2 in the diploid non-maloids studied, and GBSSI-1A, -1B, -2A, and -2B occurring the Maloideae. The sequence data, using only exon base pairs, showed that various sampled collections of Kageneckia had GBSSI-1A, -2A and -2B loci; and Vauquelinia had GBSSI-1A, -1B, -2A and -2B loci as in members of the Maloideae. Their results again showed that Kageneckia and Vauquelinia were basal to, or sister to, the "core" Maloideae.

A later report by Evans and Campbell (2002) used CBSSI gene to investigate the origin of the x=17 Maloideae. Their phylogenetic analysis of some 42 genera showed that GBSSI-1 and -2 alleles of Prunus (Amygdaloideae) were not closely associated with the Maloideae, but rather the sequences from the genus Gillenia (a herbaceous, x=9 Spiraeoid, with compound leaves and 5 separate ovaries each with 4–6 ovules that form folicular fruits with non-winged seeds) were strongly associated with, and basal to, sequences of Vauquelinia, Lindleya and Kageneckia at the base of the Maloideae clade. Gillenia has a GBSSI-1 locus that shares distinct intron deletions and additions with the GBSSI-1B loci of the Maloideae and the GBSSI-2 intron shared a distinct base pair substitution with the GBSSI-2B loci of Vauquelinia, Kageneckia and Lindleya and core Maloideae placing the diploid Gillenia at the base of the Maloideae.

Thus Gillenia would appear to be an extant survivor of a lineage ancestral to the Maloids. But what is the other parent? Their survey of the Amygdaloideae has found no potential parent. The other parent has either not been sampled or is long extinct. They conclude that the other parent could have been another x=9 Spiraeoid that, in forming a hybrid via amphiploidy, could double the chromosomes to x=18, (2n=36) and this could be reduced to x=17 (2n=34) via aneuploidy (Evans & Campbell 2002). But whatever the other parent would be, there is no reason to expect its lineage to be extant today. But definitely one of the parental lineages has a surviving member, that being Gillenia, a genus of two species native to the eastern United States.

The most recent molecular study of relationships within Rosaceae was presented by Potter et al. (2007) that investigated the relationships of 88 genera using nucleotide sequence data from six nuclear and four chloroplast regions. Their paper resulted in a complete infrafamilial rearrangement recognizing three clades as subfamilies. The basal subfamily **Rosoideae** consists of herbs, shrubs rarely trees, that lack cyanogenic glyco-

sides and sorbitol. They have alternate, usually compound, stipulate leaves; ovaries are usually numerous (rarely 1), separate, free from the hypanthium, some borne in a spiral arrangement on expanded receptacles, and the fruit are indehiscent [x=7(–8)—including *Agrimonia, Filipendula, Fragaria, Geum, Potentilla, Rosa, Rubus* etc.]. The subfamily **Dryadoideae** clade consists of shrubs, subshrubs, with cyanogenic glycosides and traces of sorbitol and a tendency to have nitrogen fixing symbionts. The leaves are simple or compound, stipulate; ovaries are 1 or many; fruits are achenes, (x = 9) including *Cercocarpus, Chamaebatia, Dryas* and *Purshia* (including *Cowania*). The Dryadoideae is sister to a highly diverse **Spiraeoideae**[1] clade consisting of mostly shrubs, small trees with some cyanogenic glycosides and strong sorbitol presence. Leaves are usually simple, alternate, the stipules persistent (deciduous in *Prunus*); ovaries number 1–5, mostly separate, radially oriented, usually free from the hypanthium, and fruits ranging from achenes, drupes, to pomes (x= 8, 9, 15, 17). It includes what was in the subfamilies Spiraeoideae (*Spiraea, Holodiscus, Petrophyton* etc.), Amygdaloideae (*Prunus*), and Maloideae (*Amelanchier, Crataegus, Malus, Pyrus* etc.) of previous classifications and several other groups.

Within the subfamily Spiraeoideae, the Maloid clade was designated in Potter et al. (2007) as the supertribe Pyrodae [the subfamily name Pyroideae Burnett (1835) named for *Pyrus*, the pear, has priority over name Maloideae Weber (1964)]. Basal in the supertribe is the genus *Gillenia* (x=9), that Evans and Campbell (2002) showed is a surviving genus of a lineage that gave rise to the Maloids. The supertribe has a single tribe, Pyreae, containing the three genera *Lindleya, Kageneckia* (x=17), and *Vauquelinia* (n=15)—its chromosome number the product of further aneuploidy and the tribe Pyreae has one subtribe, Pyrinae, that includes all the core maloids with apple-like fruits (pomes). But I see a problem with this classification. There remains no rank to distinguish the variation in the core Pyrinae (the maloids) as investigated by Lo and Donoghue (2012). And that is the subject of another paper.

***Lindleya* vs. *Vauquelinia*.**—Both *Lindleya* and *Vauquelinia* (Hess & Henrickson 1987) are moderately large, evergreen shrubs, distributed from northern, east-central to southern Mexico, with *Lindleya* ranging from northern Oaxaca to western Coahuila and the three species of *Vauquelinia* occurring from central Oaxaca to northern Baja California Norte, south-central Arizona and trans-Pecos Texas. Both genera occur in arid to semiarid scrublands, often limited to more mesic niches on north-facing slopes and along drainages or on rocky habitats where their roots can reach deeper moisture. Both have coriaceous leaves with well developed, fibrous bundle-sheath extensions with leaves of *Vauquelinia* being much larger and usually more coriaceous than those of *Lindleya*.

The smaller flowers of *Vauquelinia* are arranged in distinct well-branched compound corymbs (but see Evans & Dickinson 1999, who consider the inflorescences to be determinate, alternately branched dichasia with lateral pleiocasia similar to those found in some *Crataegus*, sensu Weberling 1989), not mostly solitary as in *Lindleya*. As in *Lindleya*, their leathery hypanthia bear five, ± thick, persistent sepals, five, white, ovate petals, (18–)20 stamens with tapered filaments, yellowish, introrse anthers and the sessile 5-carpelled ovary is mostly free from the hypanthium and topped with five separate styles, each somewhat compressed distally with broad stigmas. But unlike *Lindleya*, sepal margins of *Vauquelinia* do not contain the multicellular glands; anthers and petals are much smaller; ovaries are villous; and carpels are connate only along the inner (adaxial or ventral) margins—the outer (lateral and abaxial) margins are free (see Hess and Henrickson 1987). In *Vauquelinia*, each carpel has two basal-attached ovules (not apically attached as in *Lindleya*); the ovules, as in *Lindleya*, have two integuments, and the upper portion of the ovule develops into a wing. In *Vauquelinia*, mature fruits are more ovoid to oblong-ovoid (not ovoid-globose) in shape, and the fruit body is distinctly five lobed in cross section with five radial incisions, villous to strigose (not glabrous), but as in *Lindleya*, each carpel

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[1]The use of Spiraeoideae for the subfamily name will be altered due to the changes to Art. 19 of the Code approved in the Melborne (18th) Congress proposed by McNeill and Turland 2011 mandating priority of infrafamilial names based on the types of conserved family names over non-conserved names. Therefore the subfamily Amygdaloideae based on Amygdalaceae Marquiz (1820 nom. cons.) would have priority over names based on both Malaceae Small (1903, nom. cons.) and Spirareaceae Bertuch (1801, not conserved). However, Gunner et al. (2011) have proposed conserving Malaceae against Amygdalaceae to allow usage of the subfamily Maloideae for the subfamily.

is loculicidally dehiscent all across the ventral and distal portion of the dorsal sutures, splitting the persisting style base to shed the winged seeds. The embryos in *Vauquelinia* are about half the total seed length, are ascending, with basal hypocotyls (not two thirds the seed length with apical hypocotyls as in *Lindleya*). In both genera the seed coat is thin, brown, and endosperm is lacking. They also differ in chromosome number, with *Vauquelinia* n=15 and *Lindleya* n=17.

The South American (Chile, Peru, Brazil) *Kageneckia* (n=17) is quite distinct. The 3(–4) species are dioecious, ± large shrubs, vegetatively quite similar to some species of *Vauquelinia* in having thick, coarse leaves and occurring in dry scrublands. They have flowers ± 20–40 mm in diameter with attenuate sepals, moderately large, oblong-ovate white petals, 15–20 stamens along the hypanthial rim in male flowers but with reduced staminodia, and 5 separate vertical ovaries in female flowers, with terminal short styles and 2 rows of ovules (10–12 total) along the ventral traces. In fruit, the separate carpels expand abaxially and radiate outward to enclose the seed wings and the fruiting ovaries open along both the ventral and dorsal sutures to disperse the 10–12 winged seeds.

Spjut (1994) refers to the fruit of *Vauquelinia* as a coccetum "a multiple fruit with dehiscent fruitlets" opening along the dorsal and ventral sutures, with a note implying that the carpels are only partially connate with each carpel having a separate style-stigma. But the distinction between the fruits of *Vauquelinia* and *Lindleya* is only in the amount of lateral connation of the 5 carpels, being restricted to near the interior (ventral or adaxial) region in *Vauquelinia* but throughout the lateral surfaces in *Lindleya*. In overall structure and function, they are both loculicidal capsules. In contrast in *Kageneckia*. the carpels are completely separate, and Spjut (1994) would designate the fruit as a follicetum (i.e., a cluster of follicles) but while dehiscence occurs primarily along the dorsal suture, it continues onto the ventral suture, and his definition removes it from the follicle category, making it fit Spjut's definition of a coccetum as in *Vauquelinia*.

In molecular phylogenies that include *Vauquelinia*, *Lindleya* and *Kageneckia* [Potter et al. (2007); Campbell et al. (2007); Lo & Donoghue (2012)], *Lindleya* and *Kageneckia* are most often associated and sister to *Vauquelinia* and the rest of the pome-bearing Pyrinae. But also see Campbell 2007 for analysis of separate GBSSI genes.

APPENDIX 1

Representative Specimens: **MEXICO. Chihuahua:** Sierra de Pampas, W of Hacienda El Berrendo, 27°20'N, 104°43'W, 25 Aug 1972, *Chiang et al. 8832* (LL, NY-2); 20 km ENE Cd. Jiménez, NW summit Sierra de Chupaderos, 27°12'N, 104°43'W, 5300 ft, 2 Oct 1973, *Henrickson 13776* (TEX). **Coahuila:** E slope Sierra Almargre, 4800 ft, 5 May 1973, *Gentry & Engard 23219* (CAS, US); Vicinity of Santa Elena Mines, E foothills of Sierra de las Cruces, 30 May 1941, *Stewart 378* (F, GH, LL); Sierra Mojada, S of Esmeralda, 27°16'N, 103°41'W, 1 Sep 1972, *Chiang et al. 9086n* (LL); 23 (air) mi NW of Las Delicias, Valley N of Sierra de las Delicias, 26°23'N, 102°52'W, 4800 ft, *Henrickson 6124* (TEX); ± 29 (air) mi WNW of Cuatro Cienegas, N slope of Sierra de la Madera, 7.8 (rd) mi W of Rancho Cerro de la Madera, Cañón Desiderio, 27°08'N, 102°30'W, 12 Aug 1976, *Henrickson & Prigge 15310* (TEX); Cerro San Pedro, near N.L. line, 2 mi E of Ejido Presa de San Javier, 24°44'N, 100°46'W, 2200 m, 21 Aug 1974, *Wendt & Lott 608* (TEX); Sierra de Jimulco, 8 km NE Estacion Otto, 27 Sep 1972, *Chiang et al. 9552h* (LL); Sierra de Parras, 5500 ft, *Shreve & Tinkham 9859* (GH); 10 mi W Saltillo, near Las Barrancas, 3 May 1959, *Correll & Johnston 21400* (GH, NY, LL); Caneros Pass, 29 May 1890, *Pringle 3116* (A, F, GH, NY-2, LL). **Durango:** N end Sierra del Rosario, 20 km SW of Mapimí, 2 Nov 1972. *Wendt et al. 19035c* (LL). **Zacatecas:** 8 mi S of Majoma, 6800 ft, 4 Sep 1938, *Shreve 8581* (US); Concepcion del Oro, 2500–2700 m, 18–19 Jul 1934, *Pennell 17419* (GH, NY, US); Puerto de Rocamontes, at Zacatecas-Coahuila state line, 24°44'N, 101°10'W, 1990 m, 29 Mar 1973, *Johnston et al. 10491a* (LL). **San Luis Potosi:** 15.1 rd. mi N of Zac-SLP, hwy 49 on rd to Charcas, near Cerro Tecalote, 22°30'N, 101°09'W, 2100 m, 23 Sep 1978, *Henrickson & Lee 17553* (TEX); La Joya, 4 km NW de Ventura, Mcpio Villa Hidalgo, 1900 m, 11 Jan 1955, *Rzedowski 5705* (TEX); 20 mi S. Huizache Jct on Mex 57, 3 mi E on rd to Guadalcazar 22°42'N, 100°47'E, 5800 ft, 14 Jun 1979, *Hess & Byrne 4710* (F); E de Núñez, km 84 carretera San Luis Potosí-Antigua Morelos, 1600 m, 18 Nov 1954, *Rzedowski 5549* (ENCB). **Nuevo León:** Mts near Monterrey, Jul 1933; *Mueller & Mueller 539* (LL); 1.5 km E of El Barrosito, 1.5 km W of Puerto Prieto in S part of Sierra la Tomita, 24°36'N, 100°38'W, 2100 m, 19 Jun 1972, *Chiang et al. 8018* (CAS, NY, LL); Rd from San Rafael to Dieciocho de Marzo and Galeana, 8 mi E of San Rafael, 25°03'N, 100°25'W, 22 Oct 1982, *Dorr et al. 2500* (CAS, NY, TEX); Sierra Madre Oriental, Cieneguillas to Pablillo by upper trail, 15 mi SW Galeana, 17 Jun 1934, *Mueller & Mueller 884* (A, F, NY, TEX); 3 mi above Iturbide, rd to Galeana, 2000 m, 18 May 1949, *McVaugh 10562* (TEX, US); 13 km al E San Antonio Peña Nevada, 32°50'N, 99°57'W, 24 May 1992, *Hernandez et al. 2692* (TEX); Rancho Cielo, 11 km de Gomez Farias, 22 Sep 1974, *Medrano et al. 7425b* (GH). **Tamaulipas:** 4 km W Miquihuana, 23°42'N, 99°45'W, 3110 m, 3 Aug 1941, *Stanford et al. 626* (DS, GH, NY); 34 km N Tula, 5.5 km N of La Presita, 23°20'N, 99°39', 1700 m, 20 May 1973, *Johnston et al. 11141* (LL). **Queretero:** ca. 80 km NE of Querétaro, above Pilón, rd to Pinal de Amoles, 2700 m, 24 Apr 1949, *McVaugh 10346* (GH, LL, TEX, US). **Hidalgo:** 7 km N de Cardonal, 14 Aug 1965, *González*

2850 (DS, TEX); Cerro San Miguel, 14 km NNE de Actopan, 2300 m, 6 May 1965, *González 2401* (DS, LL); Barranca walls above Metzquítit-lan, road to Zacualtipan, 1600–1800 m, 24 Mar 1947, *Moore 2481* (GH). Puebla: Los Naranjos, May 1908, *Purpus 3234* (F, GH, NY); Mcpio Caltepec, Cerro El Mirador al SW de Coatepec, 19 Apr 1985, *Tenorio 8822* (TEX); 8 km al NE Acatepec, 16 May 1981, *Chiang et al. 1959* (TEX). **Oaxaca:** 3 km al SW de Tamazulapán sobre carr. Tamazulapán-Chilapa de Diaz, 15 May 1982, *Rico et al. 332* (F); Cerro sobre el camino de Teposcolula a San Andres Lagunas, 10 May 1981, *Cedillo et al. 770* (CAL, F); 3 km al S de Santiago Teotongo por la Terracería a San Pedro Nopala, 17°45'N, 97°33'W, 12 May 1986, *Salinas & Solis F3238* (TEX); 3 km SW de Magdalena Jicotlán a Santiago Teotongo, 97°29'N, 17°47'W, 1 Aug 1985, *Salinas & Dorado F2691* (F).

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